# Direction Of Spring Migration Of *Vanessa cardui* (Nymphalidae) In Colorado

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**Abstract.** Spring migration of 3016 *Vanessa cardui* (L.) migrants was studied in Colorado in 1992 and 1983, using standard vector methods. Migration was to the east-northeast/northeast (averaging 31° in 1992, 51° in 1983, east being 0° and north 90°), and this direction did not change significantly during the day, disproving a theory that migrants maintain a constant angle to the sun. The efficiency (unidirectionality) of migration is about 80% during peak migration, but drops to near zero afterward. Some spring adults in central Colo. overwintered there. Migrants mate-locate all day long, versus late in the day for non-migrants.

**KEY WORDS:** *Vanessa cardui*, migration, sun-compass mechanism.

## INTRODUCTION

The study of migration of butterflies is filled with numerous brief reports of vast swarms heading in a certain direction. There are fewer studies in which the direction of each individual was charted, and even fewer in which the time of day was recorded. The latter is of interest because of a theory that migrants fly at a constant angle to the sun Baker (1968a, b, 1969) and thus change direction from morning to afternoon. Recent migrations of *Vanessa cardui* allowed the testing of this theory.

## METHODS

Time of day and direction were recorded for each of 3016 adults: 2725 in 1992 and 291 in 1983. I walked about open areas (mostly large grassy areas) in metropolitan Denver, Colorado, during most hours on peak flight days but during only part of the day on some days, and estimated direction of each individual seen as one of 16 compass directions (N, NNE, NE, ENE, E, ESE, etc.).

Standard vector methods were used. Each observation represents an arrow of length 1, and the individual arrows can be drawn connected end-to-start (the start of the next vector connected to the pointed end of the previous vector) on graph paper. Then a line can be drawn connecting start of first vector to end of last vector, which forms the total vector whose length and angle can be measured from the graph paper (which represents the overall length and direction of migration). The following equations are a simpler way to calculate the length and direction of the total vector, where E is the number of adults flying toward the east, SSW the number flying toward the south-southwest, etc. (The derivation of the equations is this: for ENE for instance the angle is 22.5° and a vector of length 1 has a Y-component [height] of sin 22.5° or .3827 and an X-component [width] of cos 22.5° or .9239; and .70711 is the sin and cos of 45° for the NE vector, etc.)

X component of total vector= E - W + .70711(NE + SE) - .70711(SW + NW) +
    .3827(NNE + SSE) - .3827(SSW + NNW) + .9239(ENE + ESE) - .9239(WSW
    + WNW)
Y component of total vector= N - S + .70711(NE + NW) - .70711(SE + SW) +
    .9239(NNE + NNW) - .9239(SSE + SSW) + .3827(ENE + WNW) - .3827(ESE
    + WSW)
V (length of vector) = square root($X^2 + Y^2$)

By custom in mathematics, the directions and axes are arranged as in Fig. 1,
and angles are counterclockwise from due east (east being 0°, north 90°, west
180°, south 270°). The overall direction of migration can be found by plotting the
individual vectors, or from elementary trigonometry:
    Angle A = $\tan^{-1}(Y/X)$

The efficiency of migration is given by the length of the total vector divided by
the number of adults observed (N). It represents the proportion of individuals
that fly in the overall direction of migration (the directionality), and ranges from
1.0 if all individuals fly the same direction, to zero if flights are random in
direction. I included in sample size only flying adults, and ignored the ones
feeding on flowers or resting. Thus:
    Directionality (Efficiency) of migration E = V/N
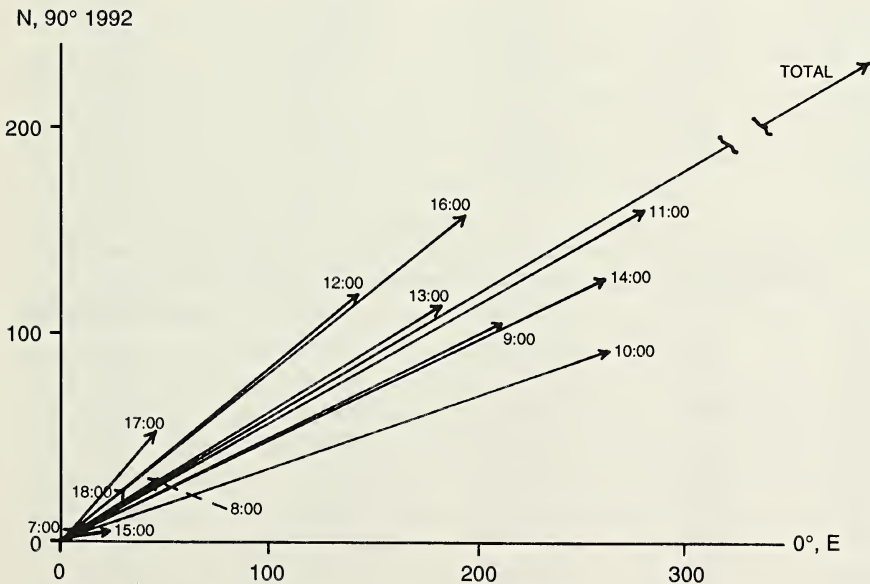    N = sample size



Fig. 1. Migration April 26-30 1992 during one-hour periods starting at the times
    indicated. A dashed line points to the 8:00 vector, and "7:00" is left of the
    7:00 vector which is hidden among the bases of the other vectors. Numbers
    on Y and X axes represent number of migrating individuals.

## RESULTS

In 1992, very few migrants (n=13) were noted from April 10-25, which flew predominantly eastward. A vast migration occurred April 26-30, few were seen May 1-2, a small migration occurred May 3, few May 4-5, few (N=18) flew northeastward May 6, and very few (N=8) flew predominantly northeastward May 8-18. Table 1 details migration from April 26-May 5. The April 26-30 peak was massive (especially April 28-30), the overall direction for the five days was a little north of ENE (31°, V=1945., N=2395), and efficiency was great (81%). May 1 the migration was ceasing (flying to NNE with only 50% efficiency), and May 2 the few adults seen were essentially nonmigratory with a very small vector and almost zero efficiency. May 3 a small migration (N=167) again occurred, but oddly its direction was southeastward at high efficiency (79%). May 4-5 few adults were seen and most were nonmigratory judging by the low efficiency (36% and 24%); they flew predominantly eastward May 4 indicating perhaps a mixture of southeastern migrants like the day before and northeastward migrants like the next day May 5 when they flew northeastward as before.

Table 1.  Daily migration 1992, N=2725.

| Day | N | Direction | Vector | Unidirectionality |
|---|---|---|---|---|
| April 26 | 57 | 25.02° | 40.27 | .71 |
| April 27 | 124 | 16.52° | 104.66 | .84 |
| April 28 | 1065 | 29.25° | 882.09 | .83 |
| April 29 | 474 | 39.51° | 382.63 | .81 |
| April 30 | 677 | 30.26° | 543.17 | .80 |
| May 1 | 53 | 63.89° | 26.65 | .50 |
| May 2 | 20 | 19.75° | 1.06 | .05 |
| May 3 | 167 | 320.34° | 132.08 | .79 |
| May 4 | 23 | 357.87° | 8.24 | .36 |
| May 5 | 26 | 41.81° | 6.28 | .24 |

Table 2.  Migration each hour April 26-May 5, 1992, N=2683. Times are military standard time of start of one hour periods (7:00 means 7:00-7:59).

| Hour | N | Direction | Vector | Unidirectionality |
|---|---|---|---|---|
| 7:00+ | 20 | 45.84° | 5.18 | .26 |
| 8:00+ | 75 | 33.94° | 53.73 | .72 |
| 9:00+ | 286 | 28.28° | 241.11 | .84 |
| 10:00+ | 361 | 22.35° | 295.22 | .82 |
| 11:00+ | 373 | 30.10° | 321.60 | .86 |
| 12:00+ | 223 | 40.40° | 185.51 | .83 |
| 13:00+ | 282 | 31.38° | 218.47 | .77 |
| 14:00+ | 422 | 23.12° | 307.54 | .73 |
| 15:00+ | 157 | 328.94° | 113.10 | .72 |
| 16:00+ | 335 | 35.29° | 250.15 | .75 |
| 17:00+ | 109 | 49.12° | 68.19 | .63 |
| 18:00+ | 40 | 39.54° | 38.98 | .97 |

Table 3. Migration each hour April 26-30, 1992, N=2395.

| Hour | N | Direction | Vector | Unidirectionality |
|------|------|-----------|---------|-------------------|
| 7:00+ | 19 | 45.71° | 6.18 | .33 |
| 8:00+ | 75 | 33.94° | 53.73 | .72 |
| 9:00+ | 274 | 26.71° | 238.13 | .87 |
| 10:00+ | 317 | 19.42° | 277.88 | .88 |
| 11:00+ | 373 | 30.10° | 321.60 | .86 |
| 12:00+ | 223 | 40.40° | 185.51 | .83 |
| 13:00+ | 268 | 31.52° | 214.07 | .80 |
| 14:00+ | 361 | 26.27° | 289.26 | .80 |
| 15:00+ | 27 | 10.24° | 20.24 | .75 |
| 16:00+ | 309 | 39.85° | 249.05 | .81 |
| 17:00+ | 109 | 49.12° | 68.19 | .63 |
| 18:00+ | 40 | 39.54° | 38.98 | .97 |
| Total | 2395 | 30.77° | 1944.63 | .81 |

Table 4. Migration 1983, in two-hour periods.

| Hour | N | Direction | Vector | Unidirectionality |
|------|------|-----------|---------|-------------------|
| 8:00+ | 45 | 51° | 11 | .25 |
| 10:00+ | 61 | 45° | 25 | .41 |
| 12:00+ | 55 | 59° | 34 | .61 |
| 14:00+ | 73 | 54° | 49 | .67 |
| 16:00+ | 57 | 42° | 42 | .74 |
| Total | 291 | 51° | 161 | .55 |

In 1983, a few adults were seen April 22-24, with a moderate migration April 25-27, few migrants April 28-30, and a small migration May 4. The overall direction of migration was to the northeast (51°, Table 4, Fig. 2).

Evidently the southwestern deserts such as the Mojave and Sonoran Deserts are the major source for spring *V. cardui* in central Colorado, if the butterflies maintained the same ENE-NE flight in Arizona-Utah-California that they flew in Colorado.

Migration in insects is generally considered to be "post-teneral, pre-reproductive" (Johnson, 1969), although there are a few observations of oviposition then continuing migration, and oviposition during north-ward migration is typical of *Danaus plexippus* (L.)(Cockrell et al. 1993); thus migration obviously starts after the cuticle is hardened for flight, and stops as the eggs become ready to be laid. This generalization seems true for *V. cardui* also, because the relative lack of migration on some days in 1992 (May 1-2, 4-5) suggests that adults had stopped migrating then, presumably to reproduce (several ovipositions were observed April 28 by a nonmigrating female).

In 1983 the efficiency of migration gradually increased during the day (Table 4), evidently because mornings were cool and adults often fed on flowers in the morning. But in 1992 efficiency was about the same all day (Tables 2-3) except very early in the morning, probably because mornings were warmer in 1992.
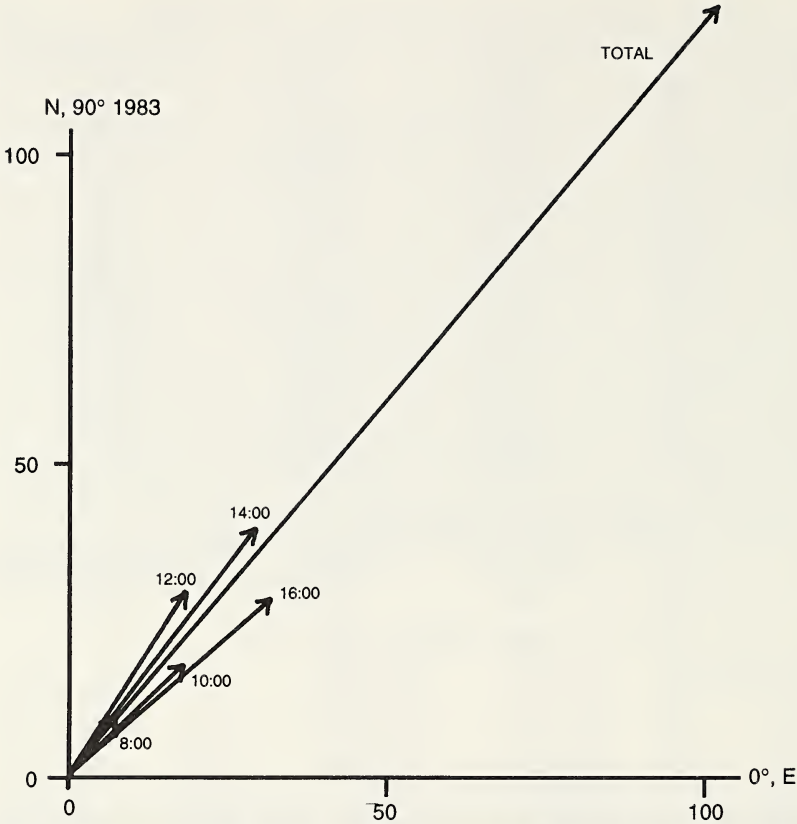
Fig. 2. Migration 1983 during two-hour periods starting at the times indicated.

## The butterfly sun-compass mechanism

Baker (1968a, b, 1969) claimed that butterflies migrate by maintaining a constant angle to the sun, so that their direction changes clockwise during the day in northern latitudes where the sun's position moves east to south to west during the day. *Vanessa cardui*, however, does not change its direction of migration during the day (Tables 2-4, Figs. 1-2). Adults flew a little north of ENE in 1992, NE in 1983, with no significant change of direction during the day. Obviously *V. cardui* has some neurological mechanism that produces a constant direction of flight during the day despite the change of direction of the sun as it moves across the sky. Probably this mechanism is the same sun-compass clock that has been demonstrated in honeybees.

The main difference between the observations of Baker and my own is that Baker recorded flight directions in ordinary populations that were not in migratory flight, and then assumed (wrongly) that their behavior was like that of migratory butterflies, whereas my observations are of obvious, definite migrations. My opinion is that Baker's observations of nonmigratory butterflies showed a change in direction during the day because glare from looking toward the sun affected the ability to notice

butterflies flying in certain directions, causing a systematic bias that followed the change of direction of the sun during the day. Possibly some non-migratory butterflies do change direction somewhat during the day, but this seems doubtful. Since no other authors have proved any significant change of direction of migration during the day, and other studies proved that direction does *not* change during the day (Arbogast 1966 on *Agraulis vanillae*, Balciunas & Knopf 1977 on *Urbanus proteus*, Walker 1978 on *Precis coenia*, *Phoebis sennae*, K. Adams in Baker 1978 on *Belenois aurota*, D. Lawrie 1984 Lepid. News #1 p. 7 and M. Myres Can. Field Nat. 99:147-155 on *Vanessa cardui*), clearly Baker's theory must be discarded.

To more-objectively determine the sun's influence on observer bias, and to obtain more accurate data, more sophisticated apparatus will be necessary: the observer would sit on a platform that rotated frequently, and would note for each migrant the compass angle printed on a surrounding deck and enter it into a computer, while the computer recorded the angle of the observer's seat to the sun; the computer would use the time of day to calculate the angles of butterfly and observer to due north, and the number of adults seen at each direction could be compared to the angle of observer to the sun to determine any observer bias.

### Adult overwintering in Colorado

Most authors have perhaps wrongly assumed that *V. cardui* overwinters only in southern areas like SW Arizona and Mexico (Williams 1970). But in central Colorado, my 30 years' observations suggest that adults almost *never* migrate southward; the very few southward migrations that have been observed were high in the mountains in midsummer (Emmel & Wobus 1966 in Colo., and I saw a southward migration in the alpine zone of Wind River Mts. Wyo. early Aug. 1983 and another in alpine central Colo.). Southward migration has never been seen on the Colorado plains/foothills, where every year during September large numbers nectar on *Chrysothamnus nauseosus* and other flowers until frost, *without* migrating. When wild-caught Sept. adults are placed in a home freezer, they die no earlier than the other *Vanessa*, *Polygonia*, and *Nymphalis* which are known to overwinter as adults (all die within 30 minutes in the freezer, suggesting that adults in nature must require many hours days or weeks of gradually colder temperatures to increase their internal concentration of glycerol to survive freezing). In addition, adults are generally present in spring even in years without noticeable in-migration, and Cockerell (1934) once found an adult in January in nature in Boulder Co. Colo. Evidence that *V. cardui* overwinters in Britain, where it was once thought to be just a temporary migrant, has been found (Baker 1978).

But analysis of wing length proves that many spring adults must be migrants from southward. In Europe, spring adults average smaller than summer adults (Baker 1978), because smaller adults bred in the

south migrate north in spring. This is also true in central Colo., where forewing length in the months from April-Oct. averages 28.9, 28.0, 29.6, 32.6, 31.2, 32.1, 31.4 mm. The main change in size is about mid June, thus April-June 10 adults average 28.1 mm (S.D. 2.9, range 21-33, N=59), whereas June 17-Oct. adults average 31.8 mm (S.D. 2.0, range 25-37, N=182). This highly significant difference (P<.01) proves that spring Colo. adults must be supplemented by migration from the south, because if spring adults were solely overwinterers they would have the same forewing length as the adults the previous fall. But some adults are large in spring (32-33 mm in both April and May) and variation in size is greater in spring (larger S.D.), and these large adults still could be overwinterers.

Probably adults hibernate in central Colorado every year, as in Europe where Baker (1978) concluded that "each autumn some individuals enter hibernation throughout the breeding range." The strength of spring versus fall migrations is reversed between *V. cardui* and *D. plexippus*: *V. cardui* migrates strongly in spring and weakly or not at all in fall, while *D. plexippus* migrates slowly northward in spring over a period of several generations, strongly southward during one generation in fall (Cockrell et al. 1993). Thus migration in *V. cardui* should not be viewed as a strictly seasonal movement like that of *Danaus plexippus*; it must be viewed also as a population outbreak in which during a few outbreak years adults fly to regions (mostly northward in spring) where prospects of rearing offspring are presumed to be better.

### Mate-locating behavior

When not migrating, *V. cardui* males mate-locate (chase others and court) only late in the day, preferably late afternoon-early evening. But during migrations they mate-locate all day: the number of chases seen each hour of migration in 1983 & 1992 was 8:00 (8:00-8:59)-4, 9:00-16, 10:00-18, 11:00-15, 12:00-12, 13:00-9, 14:00-18, 15:00-12, 16:00-25, 17:00-14, 18:00-14. No courtships were seen. Many migrations would be toward regions with a low population of adults, so mating en route seems preferable to waiting until arrival and gambling on the presence of a suitable mate there.

### Flower-feeding behavior

Adults—presumably both migratory and nonmigratory—often fed during the migrations. Yellow and white flowers may be preferred (although this may be an artifact since cultivated purple *Buddleja davidii* is enormously popular). Number of visits and flower color were: *Taraxacum officinale* (yellow) 190 visits, *Syringa vulgaris* (blue) 45 (white) 1, *Prunus cerasus* (white) 24, *Prunus virginiana melanocarpa* (white) 14, *Penstemon secundiflorus* (blue) 6, *Malus* sp. crabapple (pink) 7, *Astragalus drummondii* (white) 4, "pot of gold" mustard (yellow) 4, *Erigeron compositus* (white) 3, *Thlaspi arvense* (yellow) 3, *Prunus pissardi*

*rosea* (white) 2, *Cryptantha minima* (white) 2, *Malus sylvestris* 2 (white), *Erysimum* (yellow) 2, *Oxytropis lamberti* (purple) 1.

## LITERATURE CITED

ARBOGAST, R., 1966. Migration of *Agraulis vanillae* in Florida. Fla. Ent. 49:141-145.

BAKER, R. R., 1968a. A possible method of evolution of the migratory habit in butterflies. Phil. Trans. Roy. Ent. Soc. London (B) 253:309-341.

——, 1968b. Sun orientation during migration in some British butterflies. Proc. Royal Ent. Soc. London (A), 43:89-95.

——, 1969. The evolution of the migratory habit in butterflies. J. Anim. Ecol. 38:703-746.

——, 1978. The evolutionary ecology of animal migration. Holmes & Meier Publ. Inc., N. Y., 1012 p.

BALCIUNAS, J. & K. KNOPF, 1977. Orientation, flight speeds, and tracks of three species of migrating butterflies. Fla. Ent. 60:37-39.

COCKERELL, T. D., 1934. Pyrameis cardui on New Year's Day. Ent. News 45:174.

COCKRELL, B., S. MALCOLM, & L. BROWER, 1993. Time, temperature, and latitudinal constraints on the annual recolonization of eastern North America by the monarch butterfly. Pp. 233-251 In: Biology and conservation of the monarch butterfly, S. Malcolm and M. Zalucki eds., No. 38 Science Series, Nat. Hist. Mus. Los Angeles County.

EMMEL, T. C. & R. A. WOBUS, 1966. A *southward* migration of *Vanessa cardui* in late summer and fall, 1965. J. Lepid. Soc. 20:123-124.

JOHNSON, C. G., 1969. Migration & dispersal of insects by flight. Methuen & Co. Ltd., London, 763 p.

WALKER, T., 1978. Migration and re-migration of butterflies through north peninsular Florida: quantification with malaise traps. J. Lepid. Soc. 32:178-190.

WILLIAMS, C. B., 1970. The migrations of the painted lady butterfly, *Vanessa cardui* (Nymphalidae), with special reference to North America. J. Lepid. Soc. 24: 157-175.